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Allometric Scaling in Small Colonies of the Scleractinian Coral *Siderastrea siderea* (Ellis and Solander)

STEVEN V. VOLLMER* AND PETER J. EDMUNDS

Department of Biology, California State University, 18111 Nordhoff Street, Northridge, California 91330

Abstract. Although most physiological traits scale allometrically in unitary organisms, it has been hypothesized that modularity allows for isometric scaling in colonial modular taxa. Isometry would allow increases in size without functional constraints, and is thought to be of central importance to the success of a modular design. Yet, despite its potential importance, scaling in these organisms has received little attention. To determine whether scleractinian corals are free of allometric constraints, we quantified metabolic scaling, measured as aerobic respiration, in small colonies (≤40 mm in diam.) of the scleractinian *Siderastrea siderea*. We also quantified the scaling of colony surface area with biomass, since the proposed isometry is contingent upon maintaining a constant ratio of surface area to biomass (or volume) with size. Contrary to the predicted isometry, aerobic respiration scaled allometrically on biomass with a slope (b) of 0.176, and colony surface area scaled allometrically on biomass with a slope of 0.730. These findings indicate that small colonies of *S. siderea* have disproportionately high metabolic rates and SA:B ratios compared to their larger counterparts. The most probable explanations for the allometric scaling of aerobic respiration are (1) a decline in the SA:B ratio with size such that more surface area is available per unit of biomass for mass transfer in the smallest colonies, and (2) the small size, young age, and disproportionately high growth rates of the corals examined. This allometric scaling also demonstrates that modularity, alone, does not allow small colonies of *S. siderea* to overcome allometric constraints. Further studies are required to determine whether allometric scaling is characteristic of the full size range of colonies of *S. siderea*.

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* To whom correspondence should be addressed. Current address: Department of Organismic and Evolutionary Biology, 16 Divinity Ave., Box 90, Harvard University, Cambridge, MA 02138. E-mail: svollmer@oeb.harvard.edu

Introduction

Body size affects diverse biological variables ranging from physiological to life-history traits (Schmidt-Nielson, 1984). In unitary organisms, most processes scale allometrically (Schmidt-Nielson, 1974)—that is, they change disproportionately with size—as a result of physical and geometric constraints on body size, structure, and function (Gould, 1966; Schmidt-Nielson, 1974). Classic examples of these constraints include the limits that the skeleton places on the size of terrestrial mammals (Schmidt-Nielson, 1974; Economos, 1981) and the limits that flight muscles place on the size of flying birds (Pennycuick, 1972). Constraints often are inherent to the design of organisms, yet they can be minimized, in theory, by minor changes in geometry or shape (Brody, 1945; Gould, 1966). Profound changes in size, however, require design modifications, including elaborate structural changes and the development of complex internal systems (Gould, 1966; Schmidt-Nielson, 1984). Such changes probably evolve over relatively long time scales (Gould, 1966, 1977).

The relationship between surface area and volume is fundamentally important to scaling arguments, especially for surface-area-related phenomena such as metabolism and thermal regulation (Gould, 1966; Schmidt-Nielson, 1984), because most processes scale allometrically as a result of decreasing ratios of surface area to volume (SA:V) that are associated with volumetric increases in body size (Gould, 1966). In cases where geometric similarity is maintained with increasing size (that is, where there is geometric isom-

etry, or constancy of shape), surface area (y) scales to the two-third power of volume (x) according to the allometric equation: $y = ax^b$. This equation describes a case of functional allometry arising from geometric isometry, where a is a constant and b is the scaling exponent with a predicted value of .067 (Schmidt-Nielson, 1984; Peters, 1983). Thus, all things being equal and with geometric isometry, all surface-area-related processes (heat loss, gas exchange, etc.) also should scale to the two-thirds power of mass, *i.e.,* the surface rule (Rubner, 1883). However, most organisms do not maintain geometric similarity as they grow (McMahon, 1973), and therefore the scaling exponents of many surface-area-related processes deviate from the predicted value of 0.67 (Kleiber, 1932, 1961). Metabolism, for example, often scales to the three-quarter power in interspecific analyses ($b = 0.75$) (Zeuthen, 1953; Hemmingsen, 1960), whereas intraspecific exponents vary widely depending on the organism (Altman and Dittmer, 1968; Peters, 1983). Such deviations can be explained, in part, by geometric allometry involving changes in the shape of exchange surfaces; these changes maintain high SA:V ratios and minimize surface-area-related constraints (Gould, 1966). In an extreme case, organisms might overcome geometric constraints entirely by maintaining a constant SA:V ratio with increasing body size (Gould, 1966). However, the maintenance of a constant SA:V ratio is likely only in organisms with relatively unusual body plans—for example, the dorsoventral flattening in flatworms (Gould, 1966), and the incorporation of non-respiring biomass in corals, bryozoans, hydroids, and other colonial modular organisms (Gould, 1966; Sebens, 1987a).

It has been hypothesized that colonial modular organisms overcome the allometric constraints typically associated with volumetric increases in body size by maintaining a constant SA:V ratio as colony size increases (Jackson, 1979; Hughes and Hughes, 1986). Purportedly, this is achieved by subdividing the biomass of the colony into individual units (*i.e.,* modules) of similar size (Hughes and Hughes, 1986) and growing through modular iteration (Jackson, 1979; Hughes and Cancino, 1985). As a result, physiological processes should not be functionally constrained by declining SA:V ratios, but instead should scale proportionally (*i.e.,* isometrically, $b = 1$) to both the number of modules and the total colony biomass (Jackson, 1979; Sebens, 1979, 1987a), thereby allowing indeterminate colony growth (Sebens, 1987a). In turn, this proposed isometry is thought to be critical to the success of colonial modular organisms (Hughes and Hughes, 1986), because it should provide access to the beneficial fitness consequences of increased size (Jackson, 1977; Sebens, 1982; Hughes and Jackson, 1985; Karlson, 1988) without the constraints of allometry.

However, despite the theoretical importance of isometry in colonial modular organisms, few studies have tested this prediction, and the available data are contradictory. Aerobic respiration, for example, scales isometrically with mass in the bryozoan *Electra pilosa* ($b = 0.97$; Hughes and Hughes, 1986) but allometrically in the soft coral *Alcyonium siderium* ($b = 0.88$; Sebens, 1987b). Moreover, chemical engineering and mass transfer theory predict that many colonial modular organisms with simple geometries should display allometric scaling (Patterson, 1992a). In this study, we revisit scaling in colonial modular organisms to determine whether their body plans do, indeed, provide a comprehensive escape from allometric constraints. More specifically, we test the null hypotheses that aerobic respiration (hereafter referred to as respiration) and the surface-area-to-biomass (SA:B) ratio scale isometrically (*i.e.,* proportionately) in the scleractinian *Siderastrea siderea.* Respiration was selected to examine the scaling of physiological traits because of its importance in generating ATP for synthetic and muscular work. The SA:B ratio was selected as a proxy for the SA:V ratio because biomass (B) can be determined easily with a gravimetric approach, and it is proportional to volume with a constant tissue density.

Siderastrea siderea was used as a model system for a colonial modular taxon because, as a scleractinian, it provides a consummate example of this structural clade. Additionally, *S. siderea* is ecologically important on Caribbean reefs (Goreau, 1959) and can be identified readily to species (Foster, 1979, 1980). The study was restricted to small ($\leq$40 mm diam.), juvenile colonies (Soong, 1993) because they are tractable to investigation within the constraints of laboratory chambers designed to measure metabolism. Juvenile corals also have a strong effect on the population biology of reef corals (Bak and Meesters, 1999), and thus studies of their biology are likely to result in a better understanding of the processes driving coral demography. The full size range of *S. siderea* (to $\approx$1 m diam. and $>$100 y old, Foster, 1979) was not included because large colonies were rare at the study site (the north coast of Jamaica) and cannot be accommodated easily in laboratory apparatus. Thus, although the results of this study provide a valid test of scaling in an important life-history stage of a colonial modular taxon, the findings cannot be extrapolated beyond the size range of the colonies investigated.

Materials and Methods

Respiration

Small colonies of *Siderastrea siderea* were collected from 8.5 m depth on the forereef at Dairy Bull, about 2 km east of Discovery Bay, Jamaica, in January 1997. They were transported to the Discovery Bay Marine Laboratory (DBML) where they were epoxied (Z-Spar A-788) to tiles made of acrylic plastic. The epoxy was applied to the exposed skeleton so that only living coral tissue was left uncovered. Within 24 h, the tiles were secured to racks and returned to the collection site to recover. After more than 1 week of recovery, corals were selected haphazardly from

the racks, returned to the laboratory, and placed in a darkened container supplied with flowing seawater. The corals were kept in darkness overnight, prior to respiration measurements, to avoid the confounding effect of light history on the respiration of symbiotic corals (Edmunds and Davies, 1988).

Respiration rates were measured as oxygen flux using polarographic oxygen electrodes that were connected to an oxygen meter (Cameron OM400) and inserted into the top of clear acrylic chambers. The chambers were designed to expose the corals to unidirectional flow while retaining the minimal volumes necessary for respirometry with small organisms (Fig. 1). A small chamber was used for corals roughly 20 mm in diameter, and a large chamber for corals 21 to 40 mm in diameter. Both chambers consisted of a circular working area with volumes of 332 and 680 ml, respectively, and were regulated at ambient seawater temperature (26°C) using a water jacket and bath (Haake D1). Water flow inside the chambers was created by a stirbar rotating at a constant rate. Flow rates at the periphery of the chambers, where the corals were located, were quantified using brine shrimp cysts (Johnson and Sebens, 1993), and were not significantly different between chambers (Mann Whitney U test, $U_s = 683.5$, $n_{1,2} = 40$, $P = 0.26$). The pooled flow rate for both chambers was 5.8 ± 0.1 cm s^{-1} (mean $\pm$ SE, $n = 80$).

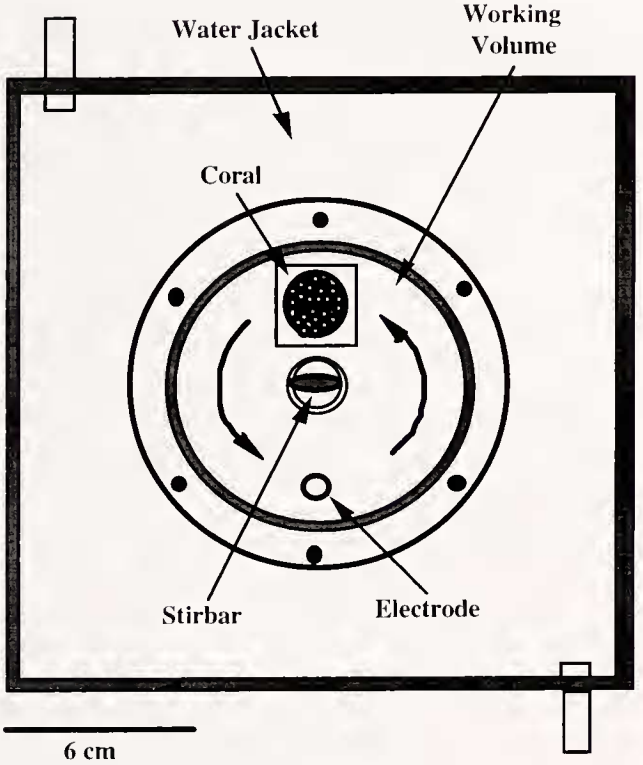

Figure 1. Plan view of the respiration chamber (drawn to scale). The chamber consisted of a cylindrical working volume (5 cm high × 14 cm in diam., 680 ml in volume) surrounded by a water jacket. A centrally located stirbar created a unidirectional flow (5.8 ± 0.1 cm s^{-1}) over the coral colony located on the periphery of the chamber; arrows indicate direction of flow.

Two oxygen electrodes were used (Strathkelvin E5046 and YSI Model 5739), and both were calibrated using a zero solution (0.01 M sodium tetraborate and sodium sulfite) and air-saturated seawater. Salinities were determined using a refractometer, barometric pressure was recorded, and oxygen solubilities were determined from Weiss (1970). Corals were placed into the chambers filled with filtered seawater (0.45 μm, FSW), and respiration rates were measured in darkness following 15-min acclimation to the chamber. All measurements were completed at an oxygen saturation above 80% (Edmunds and Davies, 1986), and data were recorded using a data acquisition system (Datacan, Sable Systems). Controls were run daily in the same manner using FSW alone. The rates of change in pO_2 in the experimental and control trials were calculated using simple linear regression ($r^2 > 0.94$). After accounting for controls, the respiration rate per coral (micromoles of oxygen per coral per hour) was calculated to examine metabolic scaling.

Surface area and biomass

After respiration measurements were completed, surface areas were estimated using the aluminum foil method (Marsh, 1970). In this technique, aluminum foil was molded over the surface of the coral; the foil was then removed, dried, and weighed; and the surface area was estimated using a previously derived relationship between area and weight. Dry tissue biomass was quantified by preserving the corals in 5% formalin in seawater, decalcifying in 5% HNO_3, and drying the resulting tissue tunic at 60°C for 7 days (Edmunds and Davies, 1986). Preliminary experiments using tissue from the anemone *Anthopleura xanthogrammica* demonstrated that the formalin and acid treatment resulted in a loss of 2.7% ± 0.7% (mean ± SE, $n = 10$) of the dry tissue. Therefore, the values of dry tissue biomass in the present study are likely to be slightly conservative.

Statistical analyses

Logarithmic linear regression was used to examine the scaling relationships. The slope of the regression provides the scaling exponent (b), and all analyses were completed using natural logarithms (ln). The scaling of metabolism was estimated by a regression analysis with the log of respiration (per coral) as the dependent variable and the log of dry tissue biomass as the independent variable. Changes in the ratio of surface area to volume were estimated by regression analysis with the log of surface area as the dependent variable and the log of dry tissue biomass as the independent variable, assuming that biomass and volume are related linearly. Model II (reduced major axis) regression analyses were used because the independent variables

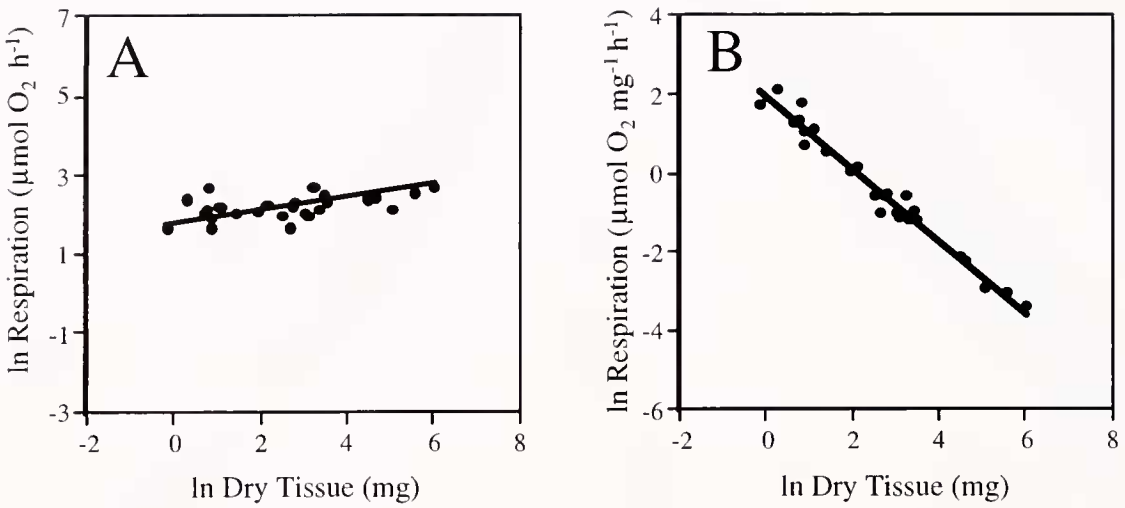

Figure 2. Respiration plotted against biomass in small colonies of *Siderastrea siderea*. (A) Regression of the log of the respiration rate per coral on the log of dry tissue biomass; regression equation: $y = 0.176\ x + 1.717$, $r = 0.499$. The slope of 0.176 ± 0.031 (±SE, $n = 26$ corals) deviates significantly from 1 ($t = 26.59$, df = 24, $P < 0.0001$), indicating allometric scaling. (B) Regression of the log of the mass-specific respiration rate on the log of dry tissue biomass (recalculated from the data in Fig. 2A); regression equation: $y = -0.924\ x - 1.9752$, $r = 0.986$.

were subject to measurement error (Ricker, 1973; Sokal and Rohlf, 1995). In this technique, the slope (or scaling exponent) is obtained by dividing the standard error of the dependent variable by the standard error of the independent variable, which results in a slope greater than that generated by least-squares linear regression (Sokal and Rohlf, 1995). The null hypothesis of isometry was tested using a t test (H_o: $b = 1$), where a significant deviation ($P \leq 0.05$) indicates an allometric relationship.

Results

Respiration

Respiration rates were estimated in 26 corals ranging in diameter between 3 and 37 mm. The regression of the log of respiration rate (micromoles of oxygen per coral per hour) on the log of colony dry tissue biomass (Fig. 2a) was significant ($F_{(1,24)} = 7.952$, $P < 0.01$), and produced a slope of 0.176 ± 0.031 (±SE, $n = 26$ corals), which deviated significantly from 1 ($t = 26.59$, df = 24, $P < 0.0001$). This significant departure from a slope of 1 indicates that respiration scaled allometrically on biomass such that respiration increased disproportionately more slowly than colony size (biomass). As a result, a doubling of biomass corresponds to only a 13% increase in the respiration rate per colony (Fig. 2a), and a 47% decline in mass-specific respiration (micromoles of oxygen per milligram of tissue per hour) (Fig. 2b).

Surface area on biomass

The scaling of colony surface area with biomass was quantified in 25 of the 26 corals; 1 coral was excluded as an outlier due to high leverage (Sokal and Rohlf, 1995). The regression of the log of surface area on the log of the dry tissue biomass of the colonies (Fig. 3) also was significant ($F_{(1,23)} = 294.973$, $P < 0.0001$), and the slope of 0.730 ± 0.041 (±SE, $n = 25$ corals) deviated significantly from 1 ($t = 6.60$, df = 23, $P < 0.0001$). This indicates that colony surface area scaled allometrically with biomass such that surface area increases disproportionately more slowly than

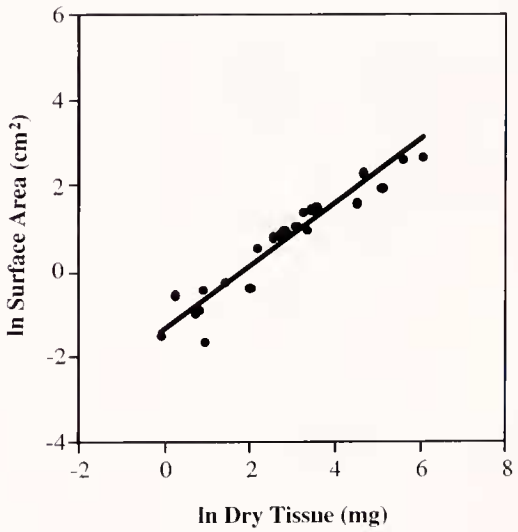

Figure 3. Colony surface area plotted against biomass in small colonies of *Siderastrea siderea*. Regression of the log of colony surface area on the log of dry tissue biomass; regression equation: $y = 0.730\ x - 1.356$, $r = 0.963$. The slope of 0.730 ± 0.041 (±SE, $n = 25$ corals) deviates significantly from 1 ($t = 6.60$, df = 23, $P < 0.0001$), indicating allometric scaling.

biomass, and the ratio of surface area to biomass declines with increasing colony size. As a result, a doubling of biomass corresponds to only a 66% increase in surface area. Moreover, the slope of 0.730 for surface area on biomass does not deviate significantly ($t = 1.453$, df = 23, $P = 0.1597$) from the expectation of geometric isometry ($b = 0.67$). Thus, the modular design of these small corals does not confer significantly higher ratios of surface area to biomass than would be expected if geometric similarity was maintained.

Discussion

Contrary to the isometric scaling predicted for colonial modular organisms (*sensu* Hughes and Hughes, 1986), respiration and surface area scaled allometrically with biomass in small colonies of *Siderastrea siderea*. As a result, both mass-specific respiration and the surface-area-to-biomass (SA:B) ratio declined with colony size. Thus, although respiration scales isometrically in at least one colonial modular organism—the encrusting bryozoan *Electra pilosa* (Hughes and Hughes, 1986)—the present results show that isometric scaling is not axiomatic with a colonial modular design. Instead, allometry describes the size-dependency of two traits in *S. siderea*, and has been demonstrated previously for respiration in the octocoral *Alcyonium siderium* (Sebens, 1987b) and predicted on the basis of chemical and mass-transfer theory (Patterson, 1992a). Although comparisons across taxa are difficult due to the wide variation in intraspecific metabolic scaling exponents, the exponent of 0.176 calculated for small colonies of *S. siderea* falls within the observed range ($b = 0.15 - 1.28$) of intraspecific exponents for metazoans (see Peters, 1983; Patterson, 1992a). Metabolic scaling exponents in unitary anthozoans range from 0.54 to 0.94 (Patterson, 1992a) and include the solitary scleractinian *Fungia scutaria* ($b = 0.79$; Krupp, 1982; exponent calculated in Patterson, 1992a). As for metabolic scaling in small colonies of *S. siderea*, we posit that the unusually small scaling exponent ($b = 0.176$) is a result of the changes in the SA:B ratio and the developmental stage of the small colonies investigated.

Maintaining a constant surface-area-to-volume (SA:V) ratio (and, with invariate biomass density, a constant SA:B ratio) is the theoretical basis for isometry in colonial modular organisms (Jackson, 1979). However, isometry can occur only where colony biomass is restricted to a single layer of modules with conserved dimensions; this design is typical of hydroids, scleractinians, and cheilostome bryozoans (Jackson, 1979). However, where there is metabolically active biomass outside the modules, the SA:B ratio decreases as extra-modular biomass increases volumetrically. Thus, the extra-modular biomass in octocorals (*i.e.*, the coenenchyme) and compound ascidians (*i.e.*, the gelatinous matrix) should favor allometric scaling (Jackson, 1979; Sebens, 1987a). These predictions are supported by experimental data from the encrusting bryozoan *Electra pilosa* and the fleshy octocoral *Alcyonium siderium* (cited above). However, although the single layer of uniformly sized polyps in scleractinians also should allow for a constant SA:B ratio, this is not the case for *S. siderea*, where colony surface area scales allometrically on biomass ($b = 0.730$). Thus, in small colonies of *S. siderea*, the SA:B ratio declines with increasing colony size, such that larger colonies have disproportionately more biomass than their smaller counterparts (Fig. 3).

The functional basis for the allometric scaling of the SA:B ratio is unknown, but it is probably related to calcification (Barnes, 1973) and the selective pressure for rapid growth in small corals (Jackson, 1977). Thus, the smallest corals may sustain high rates of linear growth (*i.e.*, calcification) at the expense of tissue growth, so that the existing tissues are "stretched" thinly over the increasing surface area. Then, as the colonies become larger, they may concentrate resources on tissue growth, thereby increasing biomass and tissue thickness. Support for this hypothesis comes from two studies. First, reanalysis of the data of Jokiel and Morrisey (1986) for the coral *Pocillopora damicornis* demonstrates allometric scaling of surface area with biomass ($b = 0.700 \pm 0.057$, mean $\pm$ SE, $n = 6$) as well as respiration ($b = 0.840 \pm 0.041$, mean $\pm$ SE, $n = 6$) (Jokiel and Morrisey, 1986). Thus, biomass is added more rapidly than surface area and, as in *S. siderea*, the resulting allometric scaling of the SA:B ratio provides a possible explanation for the allometric scaling of respiration in *P. damicornis*. Second, trade-offs in growth between skeleton and tissue, similar to those proposed for *S. siderea* (described above), have been reported for *Porites* from the Great Barrier Reef (Barnes and Lough, 1993), as have systematic differences in tissue thickness for the same species (Barnes and Lough, 1992). Indeed, the positive relationship between tissue thickness and colony height in *Porites* (Barnes and Lough, 1992), together with the large amount of extra-modular biomass (≈90% by thickness, Barnes and Lough, 1992), might be prominent in this genus. Thus, variation in tissue biomass, thickness, or both with colony size may be a general feature of scleractinian corals. However, in addition to putative changes in tissue thickness driving the observed changes in the SA:B ratio, it is possible that the SA:B ratio was biased by the use of the aluminum foil method (Marsh, 1970) to measure the surface area. This technique is widely used for determining the surface area of corals with relatively smooth and unconvoluted surfaces like those in *S. siderea* (see Hoegh-Guldberg, 1988, for an alternative approach), but it is unable to quantify the area of the expanded polyps. Quantifying the area of expanded polyps is made difficult by their highly variable morphology and degree of expansion and, as a result, previous studies have relied on geometric approximations to obtain polyp or

tentacle area (Sebens, 1981). Regardless of the methodological difficulties, currently there is no evidence of systematic variation in polyp dimensions with colony size (*i.e.*, allometry); moreover, polyp dimensions may be highly conserved for mass-transfer purposes (Patterson, 1992a). Thus, given that the thickness of coral tissues is known to vary (*e.g.*, Barnes and Lough, 1992), we believe that changes in the SA:B ratio are more likely to be driven by tissue thickness than by the area of expanded polyps. Still, a definitive test of the hypothesized mechanism of variation in the SA:B ratio is required, and this will necessitate an analysis of tissue thickness and skeletal extension as a function of colony size.

The allometric scaling of the SA:B ratio in *S. siderea* could drive the scaling of respiration through indirect effects on mass transfer of metabolites to the coral tissue. Mass transfer with the surrounding seawater is determined, in part, by surface area, which decreases relative to biomass as *S. siderea* increases from 3 to 37 mm in diameter. Thus, all things being equal (*i.e.*, excluding the boundary layer arguments described below) and within the size range studied here, small corals should maintain relatively higher fluxes of metabolites than large corals, which could support the higher respiration rates observed in the small corals (Fig. 2). Additionally, increases in biomass will be accompanied by increases in biovolume that probably lengthen diffusion pathways (*i.e.*, the tissue thickness) and reduce the rates of solute transport (Patterson, 1992b). For the colony size range studied, the respiration of large *S. siderea* therefore may be depressed by limitations on the delivery of oxygen to metabolically active tissue. This hypothesis could be tested by measuring the magnitude of the flow dependency of respiration (*sensu* Patterson and Sebens, 1989), with the expectation of a greater effect in larger colonies than in smaller ones.

Although the scaling of the SA:B ratio provides a testable hypothesis to explain the scaling of respiration in *S. siderea*, it does not exclude the possibility that other factors might also be important. Of these, variation in energy expenditure among developmental phases (*i.e.*, colony sizes) has the greatest potential to explain, in part (or entirely), the allometric scaling of respiration. In benthic marine invertebrates, scaling exponents typically are affected by the size range and developmental phase of the organisms investigated (Zeuthen, 1953). Lower exponents are characteristic of early and late developmental phases and of the extremes of the natural size range. For example, metabolic scaling exponents (b) for the mussel *Mytilus edulis* change from 0.80 in recruits (<0.1 mg) to 0.95 in sub-adults (0.1 to 1 mg) and to 0.65 in adults (>1 mg) (Zeuthen, 1953). The low scaling exponents in the smallest (*i.e.*, youngest) size classes demonstrate that their metabolic rates are relatively high compared to those of the larger sub-adults, and are thought to be a consequence of the elevated energy expenditure necessary to sustain accelerated growth (Zeuthen, 1953). Size and age are poorly related in scleractinians (Hughes and Jackson, 1980), but the colonies of *S. siderea* used in the present study (≤37 mm diam.) are young relative to the largest colonies of this species (≈1 m diameter and >100 y old; Foster, 1979), and the smallest corals (3 mm diam.) may be only a few months old (Van Moorsel, 1988). Regardless of age, small corals are probably exposed to selective pressure for rapid growth (Jackson, 1977), as occurs in other colonial modular organisms (Jackson, 1977; Sebens, 1982; Karlson, 1988), because of the mortality risks of being small (Jackson, 1977). Thus, in addition to the SA:B explanation for allometric scaling in small colonies of *S. siderea* (described above), it is possible that the respiration rate (per coral) in the smallest colonies is elevated by the high metabolic rate of young tissues or by the costs of responding to the selective pressure for rapid growth.

Two other hypotheses could account for allometric scaling of respiration in small colonies of *S. siderea*—namely, mass transfer effects (*sensu* Patterson, 1992a) and the populations of endosymbiotic zooxanthellae—but these are not supported by the available data. The "mass transfer hypothesis" focuses on the importance of mass transfer in moving metabolites between the coral tissue and seawater and driving coral respiration (Patterson and Sebens, 1989; Patterson *et al.*, 1991). The boundary layers next to the coral have a critical role in determining rates of mass transfer (Denny, 1988; Patterson, 1992b) and are a function of the interaction of the flow regime with the size and shape of the coral colony. Based on these relationships, Patterson (1992a) predicted that metabolic scaling in aquatic organisms could be explained with a mass transfer argument. In short, changes in organism size and shape can be sufficient to alter mass transfer and support the allometric scaling of metabolism, with exponents similar to published values (Patterson, 1992a). For hemispherical objects like the small colonies of *S. siderea* used in the present study, the mass transfer explanation for metabolic scaling (*sensu* Patterson, 1992a) would predict an exponent (b) of ≈0.47 (Helmuth *et al.*, 1997). This is 2.7-fold higher than the allometric scaling exponent we calculated for respiration in small colonies of *S. siderea* that have hemispherical colonies (b = 0.176). One reason for this discrepancy is that the colonies used (3–37 mm diam.) were probably too small to establish their own equilibrium boundary layers (Denny, 1988) and were, instead, affected by upstream roughness elements in the respiration chamber (Gardella and Edmunds, unpubl. data). In other words, small colonies of *S. siderea* may be an exception to the mass transfer argument for allometric scaling (*sensu* Patterson, 1992a), because they all are too small (*i.e.*, ≤37 mm diam.) to affect their own boundary layers directly.

The "zooxanthellae hypotheses" focus on the role of the zooxanthellae in contributing to the respiration of the col-

ony (*i.e.*, the cnidarian host plus algal symbionts) (Muscatine *et al.*, 1981; Edmunds and Davies, 1986) to account for allometric scaling of coral respiration. Thus, changes in the density or metabolic activity of zooxanthellae should affect the respiration of the colony and, if these changes are correlated with size, could affect metabolic scaling. In *S. siderea*, zooxanthellae densities cannot account for allometric scaling of respiration, because zooxanthellae densities scaled isometrically with biomass (Vollmer, 1999). It is possible, however, that the respiration rate per zooxanthella varied with colony size, but this possibility cannot be examined experimentally at the current time because zooxanthellar respiration can only be measured *in vitro*, and these rates may be different from those attained *in hospite* (Gates *et al.*, 1999). In the absence of *in hospite* determinations of zooxanthellar respiration, and given that zooxanthellae densities scale isometrically, we conclude tentatively that the zooxanthellae are unlikely to be a proximal cause of the allometric scaling of respiration in small *S. siderea*.

This study demonstrates allometric scaling in small colonies of *Siderastrea siderea* and underscores two mechanisms that probably drive this scaling—*i.e.*, disproportionate changes in the SA:B ratio and the developmental stage of the colonies examined. Because both mechanisms may be associated with the rapid growth necessary to escape the risky life-history stage of being small, allometric scaling probably has strong fitness consequences. While it remains to be seen whether the present findings are applicable to other species, or to a larger size range of colonies, further studies of allometric scaling in scleractinians will be valuable.

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